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Observations on the biology of *Eooxylides tharis* (Lepidoptera: Lycaenidae)

by

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Abstract: Males of *Eooxylides tharis* (GEYER [1837]) occupy perches on sunny spots near the hostplant, *Smilax barbata* (Smilacaceae). Females are also most often seen near hostplant patches. Both sexes visit extrafloral nectaries and drink plant sap at feeding damage caused by conspecific caterpillars. Oviposition occurs singly on the youngest hostplant parts. The well camouflaged caterpillars feed only on young, developing leaves and shoots. They possess a nectary organ and eversible tentacles and are facultatively attended by various ant genera (*Crematogaster, Meranoplus, Anoplolepis*) during the third and fourth instar. L_3 and L_4 larvae as well as pupae produce substrate-borne vibrations. The observations are compared with available life-history data for members of the subtribes Loxuriti and Cheritriti.

Beobachtungen zur Biologie von *Eooxylides tharis* (Lepidoptera: Lycaenidae)

Zusammenfassung: Männchen von *Eooxylides tharis* (GEYER [1837]) besetzen Warten (sonnenbeschienene Blätter etc.) in der Nähe ihrer larvalen Wirtspflanze (*Smilax barbata,* Smilacaceae). Auch die Weibchen werden am häufigsten in der Nähe dieser Pflanzen beobachtet. Beide Geschlechter saugen an extrafloralen Nektarien ihrer Wirtspflanze und von Ingwergewächsen. Auch Saft an Fraßstellen der Raupen dient den Faltern als Nahrung. Die Ablage der porzellanweißen, charakteristisch geformten Eier erfolgt einzeln an ganz junge Blätter und Triebe von *Smilax.* Die Anwesenheit von Ameisen ist bei der Eiablage nicht erforderlich. Eier und Raupen sind fast permanent von Ameisen umgeben, die die Nektarien der Wirtspflanzen besuchen. Im 3. und 4. Stadium besitzen die Raupen ein dorsales Nektarorgan und paarige Tentakelorgane. Sie sind dann fakultativ myrmekophil und werden stetig von verschiedenen Ameisen besucht (*Crematogaster, Meranoplus, Anoplolepis*). Raupen (L_3 und L_4) und Puppen produ-

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zieren substratgetragene Vibrationen, insbesondere bei mechanischer Reizung. Die Falter und Präimaginalstadien werden abgebildet, und die Beobachtungen an *E. tharis* werden im Vergleich zu biologischen Daten weiterer Arten der Subtriben Loxuriti und Cheritriti diskutiert.

The hairstreak butterfly subtribe Loxuriti SWINHOE 1910 is a small, well-defined unit among the Oriental Lycaenidae. Following ELIOT (1973, 1992) and BRIDGES (1988), the Loxuriti comprise 6 genera with 19 described species. There are morphological affinities to the subtribes Horagiti SWINHOE 1910 (with two included genera comprising about 13 species) and Cheritriti SWINHOE 1910 (7 genera with ca. 24 species). The phylogenetic relationships between these 3 subtribes and their included genera are not resolved. In addition, similarities in wing patterns also exist between certain Oriental genera currently assigned to the subtribe Iolaiti RILEY 1956 (e.g. *Jacoona* DISTANT 1884, *Neocheritra* DISTANT 1885, *Thrix* DOHERTY 1891, *Manto* DE NICEVILLE [1895], *Mantoides* DRUCE 1896) and members of the Cheritriti (like *Cheritra* MOORE 1881, *Ticherra* DE NICEVILLE 1887, *Drupadia* MOORE 1884). Therefore, a satisfactory systematic arrangement of these attractive butterflies requires utilization of cladistic methodology involving as many species and characters as possible. Biological data and morphological characters of early stages should be particularly helpful, but are poorly documented for most of the species in question.

As far as known today, the larvae of Loxuriti species share one remarkable synapomorphy: they feed on young growth of 2 monocotyledoneous families, viz. Smilacaceae and Dioscoreaceae (ELIOT 1992). In general, monocots are rarely used as hostplants by members of the family Lycaenidae. A number of records of monocot hostplants refer to exceptional findings in polyphagous species or to single hostplant specialists in groups that otherwise utilize more "usual" hostplants (FIEDLER 1991 a). Specializations of whole lycaenid clades on monocot hostplants are very rare (e.g. some *Hypolycaena* C. & R. FELDER 1862 species on Orchidaceae: FIEDLER 1992 a).

Here I report observations on adult behaviour and preimaginal biology of *Eooxylides tharis* (GEYER [1837]) in Peninsular Malaysia. The larval hostplant, *Smilax barbata,* has already been reported in 1956 (together with a rough description of the caterpillar: ELIOT 1992), but since then almost nothing appears to have been published about the biology of *E.*

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tharis. The species is distributed from southernmost Myanmar and Thailand across the Malay Peninsula (including Singapore and the Tioman Islands) to Nias, Siberut, Sumatra, Borneo, Palawan and adjacent smaller islands (SEKI et al. 1991) eastwards to Java, the type locality of the nominate subspecies *tharis* (GEYER [1837]). Populations of the Malay Peninsula can be referred to as ssp. *distanti* RILEY 1942, specimens from northern Borneo as ssp. *tharisides* FRUHSTORFER [1904].

Observations were made in 1988 and in the years 1991–1993 in the Gombak valley, about 20 km northwest of the Malaysian capital Kuala Lumpur. This area is predominantly covered with advanced secondary forest of the lowland dipterocarp type at elevations of 200–400 m.

Habitat and adult behaviour

Adults of *E. tharis* occur along forest paths, roadsides or in forest gaps, where the hostplant grows (also ELIOT 1992). Perching males are never found far away from hostplant populations. The hostplant, *Smilax barbata* (taxonomy following HENDERSON 1974), is common in disturbed successionary microhabitats like forest edges or gaps. Adult males perch on exposed points such as large leaves or ends of twigs, mostly 1–5 m above ground. From these perches they rapidly start to chase any larger flying insects that approach. If the intruder is a conspecific, a typical co-rotating flight (SIBATANI 1989) commences, after which one butterfly (presumably the "owner" of the perch in most cases) usually returns after some time. If a male has left his perch to approach a non-conspecific insect (e.g. nymphalid butterflies, dragonflies), he immediately returns to his perch after "recognizing" his "error". Sometimes 2–5 males occupy perches along the margin of a single forest gap or in neighbouring sunny patches along a wayside. Females can also be observed in the vicinity of their hostplant, either in searching flights for oviposition sites or resting in the vegetation.

The way *E. tharis* butterflies obtain their food is remarkable. I have not yet seen a single flower visit, nor did I observe males puddling on moist soil or similar mineral sources. Instead, I have repeatedly observed males and females at extrafloral nectaries of wild gingers. Extrafloral nectaries (EFNs hereafter) are apparently unrecorded from Zingiberaceae, but are well-known from the related families Costaceae and Marantaceae (KOPTUR 1992; also ELIAS 1983). On the gingers in question (a generic determination was impossible, because no flowers

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were available), the nectaries are located above the base of the leaf stalk and are conspicuous due to their reddish or purplish colour (Fig. 2). Ants of various genera (e.g. *Rhoptromyrmex, Polyrhachis, Technomyrmex*) and flies often visit the EFNs which appear to be most attractive on young foliage. Adults of the lycaenid butterfly *Logania malayica* DISTANT 1884 (Miletinae) likewise drink from these EFNs (FIEDLER 1993).

On 10. ix. 1992, 11.30 local time, I first noted a female *E. tharis* alighting on a ginger plant and drinking at an EFN. She uncoiled her relatively short proboscis and intensively licked across the plant surface for more than 10 min. Occasionally, an ant (*Technomyrmex* sp., Dolichoderinae) approached, but there was little interference and the female did not leave. A small fly was likewise attracted to the same EFN (Fig. 2). The observation and photographic documentation was interrupted at 11.45, when the female still sucked at the EFN. At 13.00 (90 min after the initial observation), a female *E. tharis* (most likely the same individual) sat on the same ginger leaf. Now she rested in a hanging position on the underside of the leaf blade, because it had started to rain. On 20. ix. 1992 I observed another 3 adults at the same locality drinking on ginger EFNs, one being accompanied by a *Technomyrmex* ant. A fourth butterfly rested at an EFN.

I also observed adult *E. tharis* at the EFNs of the larval hostplant, *Smilax barbata*. EFNs of Smilacaceae are known in the botanical literature (KOPTUR 1992). They occur on very young, reddish leaves. These leaves are fleshy and tender, contrasting to the leathery mature foliage. Ants of various genera steadily visit the EFN-bearing *Smilax* shoots (*Meranoplus mucronatus, Crematogaster* spp., *Hypoclinea* spp., *Oecophylla smaragdina, Anoplolepis longipes*). On 10. ix. 1992 (11.00) a female intensively licked such a shoot with its proboscis for about 10 min. This shoot was already infested by *E. tharis* larvae, and the female also sucked at the caterpillars' feeding damage where plant sap issued out (Fig. 3).

On 22. iv. 1993, Dr. D. KOVAC and Dr. K. RIEDE (pers. comm.) observed and photographed a female of *E. tharis tharisides* in Poring (East Malaysia, Sabah, 500 m). The female sat on a *Smilax* shoot together with eggs, egg shells, a second instar larva and tiny *Tapinoma* ants. Possibly she also searched for plant sap or nectar.

I have observed only one attempt to lay an egg and one successful oviposition act. On 30. viii. 1992, 15.00, a female performed the usual

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searching flight, then alighted on the tip of a very young *Smilax* shoot and examined the plant surface with her antennae. Finally, she curled the abdomen and dragged the abdominal tip across the plant, but flew off before laying an egg. No ant was at that time present. A complete oviposition sequence was observed on 30. i. 1988 around noon, in the presence of the ant species *Anoplolepis longipes*.

I have often found the conspicuous white eggs or egg shells. Eggs are only laid on the fleshy young tip of *Smilax* shoots. Older leaves and twigs are strictly avoided. Most appropriate shoots receive larger numbers of eggs and egg shells. Three neighbouring shoot tips censused on 30. viii. 1992 had a total of more then 30 eggs plus egg shells. Another shoot, collected on 25. iii. 1993 at Fraser's Hill (1250 m), carried 3 egg shells, 2 eggs and one L_1. The *Smilax* shoot from Poring (leg. D. KOVAC) had 5 egg shells and one L_2. This does, however, not indicate egg-clustering. In captivity, the caterpillars asynchronously hatch from the eggs on a single shoot over 2–3 days. Hence, higher egg numbers are most likely due to multiple visits of the same female, or various females, on subsequent occasions. Eggs are almost universally accompanied by ants that visit the hostplant's EFNs, but the ants pay no attention to them.

Immature stages

The egg of *Eooxylides tharis* has a unique shape (Figs. 1 & 4). It is hemispherical with the upper pole surrounded by a circular elevated ring. In a depression amid this ring the micropyle region is found. The egg is of a shining porcelain-white and has a basal diameter of 1 mm. From eggs collected on 30. viii. 1992 at Ulu Gombak, L_1 larvae hatched on 2. ix., and from eggs sampled on 17. xi. 1991 in the Genting Highlands larvae hatched on 20./21. xi., indicating an egg period of 3–4 d.

When hatching, the first instar larva is whitish. L_1 caterpillars feed by scraping the external tissue of youngest and very tender leaves and shoots of *Smilax barbata*. Some L_1 and L_2 larvae also bore into fleshy hostplant parts. After 2–3 d, the larvae moult into the second instar. L_2 larvae (final length 4 mm) are either uniformly ochreous yellow or red (Figs. 4 & 5), depending on the colour of their hostplant, and likewise feed by scraping. The second instar lasts 3–4 d.

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Third instars vary from deeply red to ochreous yellow and lack distinct colour markings. They are rather flat with a humpbacked thorax and are somewhat waisted at the central abdominal segments. Fourth (= final) instar larvae retain this shape and polychromism (Fig. 6). Most larvae found in the field were entirely red, but others had a green tinge of various extent, and one was almost entirely green. At a first glance the caterpillars appear to be "naked". Inspection under a stereo microscope, however, reveals that mature larvae possess a large number of setae. On either side of the prothoracic shield there is one long filiform seta, and on the lateral parts of T2 and T3 there are small areas with short, stiff sensory bristles. Otherwise, the caterpillars have almost no hairs with a prominent shaft (except a few around the opening of the dorsal nectary organ), but they are evenly studded with large numbers of pore cupola organs. These are hair-derived glands are involved in myrmecophily and bear a terminal sieve plate replacing the hair shaft. The myrmecophilous third and fourth instars (see below) have a dorsal nectary organ on A7 and a pair of short, eversible tentacle organs on A8. Mature larvae reach a length of 14 mm. Fourth instars sampled in the field took another 4–5 d to pupate in captivity.

The girdled pupa (length 13 mm)(1) is terminally attached to the substrate with a large plate-like structure derived from the posterior abdominal sternites and the cremaster. The whole plate is covered with hook-like setae which firmly fix the pupa to the silk pad which the larva spins prior to pupation. In captivity, pupation took place on host-plant twigs, from which the pupa projects like a bud. The pupa (Fig. 7) has a green ground colour, the wing cases are darker with a whitish tornal corner. Along the edge of the wing cases there is a purple tinge. A row of dark dots is situated mid-dorsally on the abdomen, and the spiracles are yellowish and conspicuous (especially on the prothorax). The pupal stage lasted 12–13 d in captivity.

Akin to the mature larva, the pupa is evenly studded with very numerous pore cupola organs. A group of erect bristles accompanies the spiracle of A6. Otherwise longer setae are absent. The contact zone

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(1) = In contrast to ELIOT's (1973) statement that Loxuriti pupae would lack a girdle, at least the species *Eooxylides tharis* and *Yasoda pita* (HORSFIELD [1829]) have girdled pupae (pers. observ.). According to ELIOT (loc. cit.), pupae of Cheritriti would likewise lack a girdle, but girdled pupae have been found in *Drupadia ravindra moorei* (DISTANT 1882) and *Cheritra freja* (FABRICIUS 1793) (FIEDLER & SEUFERT, unpublished).

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between abdominal segments 5 and 6 is highly modified and flexible, allowing the rapid movements associated with the defensive "knocking" behaviour (see below).

Myrmecophily and substrate-borne vibrations

Eggs as well as first and second instar larvae usually live in close proximity to ants that visit the hostplant's EFNs, but are hardly attractive to ants. Third and fourth instars are truly myrmecophilous, being equipped with very numerous pore cupolas, a dorsal nectary organ and tentacle organs. One third instar observed in the field was intermittently tended by a *Crematogaster* worker (Myrmicinae) (Fig. 3). This loose association continued in captivity. Mature larvae are highly attractive to ants. On 17. i. 1988, 6 L_4 of different size were found (together with Prof. U. MASCHWITZ) that were all intensively antennated by *Anoplolepis longipes* ants (Formicinae). Three L_4 caterpillars were observed on 14. xi. 1991 in close association with the ant *Meranoplus mucronatus* (Myrmicinae). These caterpillars were literally covered by 3–6 ants each. When the larvae were transferred into rearing vials together with their original tending ants, the *Meranoplus* workers continually tended the larvae until pupation over 4 d. Secretions from the DNO were frequently observed, and at least one ant permanently sat at the glandular opening. Further ants antennated the whole body and pressed their mouthparts against the cuticle, presumably harvesting the secretions of the pore cupola organs.

Mature larvae often extruded their tentacle organs, especially when molested (e.g. when a caterpillar was handled with forceps, or when deprived of their ants on the stethoscope or under a microscope). *M. mucronatus* showed a distinct behavioural reaction following TO eversions: either the ant rapidly jerked towards the rear end of the caterpillar, or, more rarely, the ant jerked back.

Third and fourth instars produce substrate-borne vibrations. Third instar larvae not always showed vibratory behaviour when tested, whereas mature larvae readily did. The vibratory signals were detected using a stethoscope. The acoustic impression was that of an irregular "crackling" or "croaking" noise. Two frequency components (a lower ground vibration and a higher "snarling") were clearly separable. The caterpillars made vibrations after handling, but stopped vibrating when molested very heavily.

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Pupal vibrations also occur. Two pupae were repeatedly tested on a stethoscope on the second, fourth and seventh day after pupation, but neither substrate-borne vibrations nor air-borne stridulations could be recognized. On the ninth day, however, both pupae produced faint clicking pulses (2–3 per second) after lateral tactile stimulation with forceps. The clicking noise was audible through the stethoscope as well as through air, when the pupae were placed on the stethoscope membrane. The clicking behaviour faded away quickly. On the followning day (tenth day of pupal stage, both pupae now had pigmented eyes) the same vibrations were again observed, but only in one of the pupae.

In addition, the pupae showed another response to heavy tactile disturbance: they "knocked" by rapidly moving their head against the substrate. The resulting vibrations were well perceivable using a stethoscope, but air-borne "sound" also occurred. Knocking could be stimulated by pinching the pupal thorax laterally or dorsally with forceps. After each disturbance, only 2–5 knocking events occurred, and the behaviour faded off soon. Knocking was first observed on the ninth day of the pupal stage and was confirmed on the subsequent day in both available pupae.

Discussion

The observations on adult behaviour suggest that *Eooxylides tharis* males use perching as mating strategy. Since perches were always near larval hostplants (*Smilax barbata*), this could represent a case of resource-based territoriality (LEDERHOUSE et al. 1992). Most butterflies, including the few lycaenid species hitherto studied, exhibit non-resource-based territoriality (e.g. CORDERO & SOBERON 1990, RUTOWSKI 1991). I have repeatedly observed perching behaviour in males of the closely related *Loxura atymnus fuconius* FRUHSTORFER [1912] as well as in *Drupadia ravindra moorei*. It remains to be seen whether male territoriality is a mating strategy common to the whole clade comprising Loxuriti, Cheritriti and Horagiti.

To obtain food, *E. tharis* butterflies visit EFNs instead of flowers, although I cannot rule out that flower visits or mud-puddling do occur occasionally. Drinking at EFNs has rarely been reported in adult butterflies (KOPTUR 1992), whereas larvae of certain Riodinidae and Lycaenidae regularly exploit EFNs (DEVRIES & BAKER 1989, DEVRIES 1991 b, FIEDLER 1992 b). We have observed adults visiting EFNs also

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in *Drupadia theda thesmia* (HEWITSON [1863]) and *Drupadia ravindra* (SEUFERT & FIEDLER, unpubl.). The Arhopaliti species *Surendra vivarna* (HORSFIELD [1829]) and *S. quercetorum* (MOORE 1858) likewise visit EFNs (LARSEN 1987, SEUFERT, pers. comm.), as do certain members of the subfamily Miletinae (*Allotinus unicolor* C. & R. FELDER [1865], *A. leogoron* FRUHSTORFER 1916, *Logania malayica:* FIEDLER 1993 and unpubl.). Therefore, this way of food acquisition may be more common among the Lycaenidae.

In the subtribes Loxuriti and Cheritriti, adult butterflies have all a rather short proboscis. This probably limits access to floral nectar, but would be advantageous in collecting extrafloral nectar. Since many Lycaenidae species interact with ants during oviposition, this butterfly family appears "pre-adapted" to utilize extrafloral nectar more broadly. *E. tharis* is not deterred by ants during oviposition, and the related *Loxura atymnus fuconius* has also been observed to lay eggs among *Anoplolepis longipes* ants without any aggressive interference (MASCHWITZ & FIEDLER, unpubl.).

E. tharis butterflies also sucked plant sap at feeding damage caused by the caterpillars. This behaviour has yet only been reported by DEVRIES (1984) for *Curetis regula* EVANS 1954. Since ants often visit such feeding marks (e.g. DEVRIES 1984, observations of P. SEUFERT on *Ch. freja*), this again requires peculiar adaptations to co-exist with ants.

The observations on larval biology confirm that *E. tharis* is steadily myrmecophilous (FIEDLER 1991 b) in the later instars. However, there is no specific relationship towards ants. *E. tharis* utilizes a niche where ants are almost permanently present due to the hostplant's EFNs. Therefore, the larvae probably receive protection through their ant guard ("enemy-free space" of ATSATT 1981), which they reinforce with the help of their own myrmecophilous glands. No parasitoids were reared from larvae sampled in 3 different years, suggesting a low incidence of larval parasitoids. In contrast, eggs are heavily attacked by minute hymenopterans (probably Trichogrammatidae).

The relationship of *E. tharis* and other Loxuriti species to their monocotyledoneous hostplants (Smilacaceae and Dioscoreaceae) is exceptional among the Lycaenidae. Together with the great similarities between the early instars, this hostplant association provides strong support for the monophyly of the Loxuriti. In favouring the youngest, most nutrient-rich parts of the hostplant, *E. tharis* well fits into the concept

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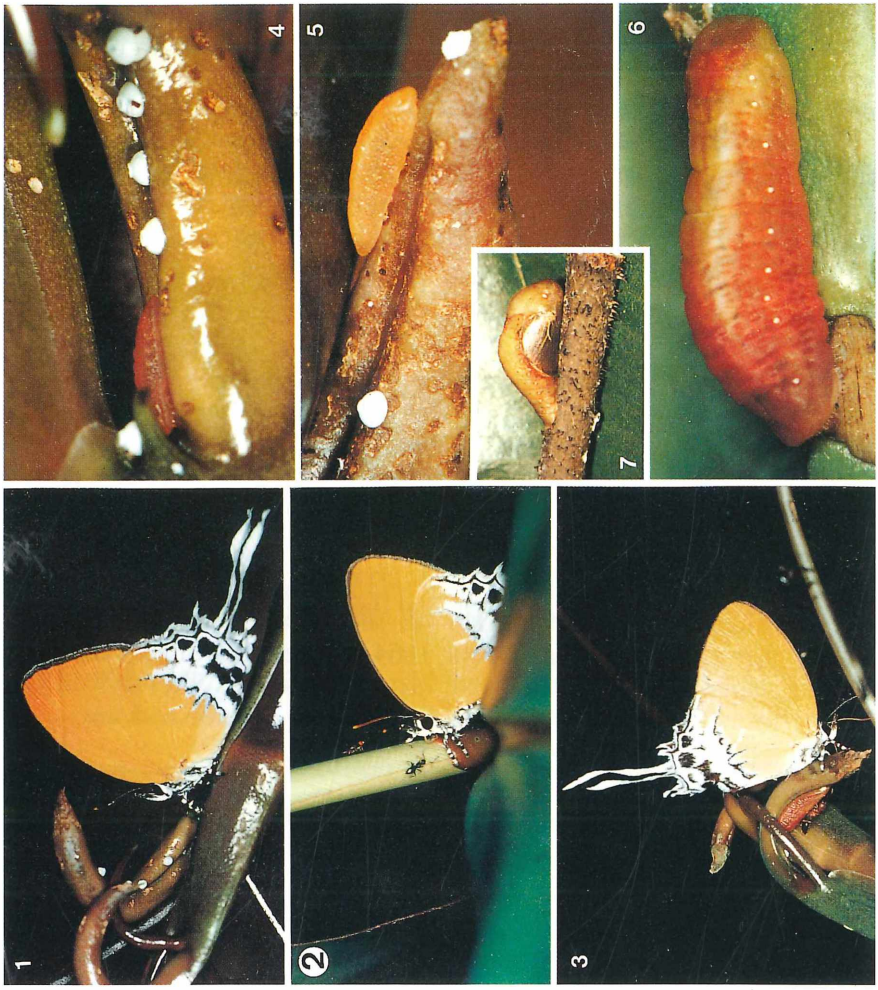

Colour plate: *Eooxylides tharis*. **Fig. 1:** Female on young shoot of *Smilax barbata*, with white eggs. **Fig. 2:** Female *E. tharis* at extrafloral nectary of wild ginger. A *Technomyrmex* ant and a small fly are also attracted to the nectary. **Fig. 3:** Female sucking at feeding damage of caterpillars on *S. barbata*. A red third instar caterpillar is present on the same shoot, attended by a *Crematogaster* ant. **Fig. 4:** Red colour morph of second instar larva. Note the characteristic shape of eggs. **Fig. 5:** Yellowish colour morph of second instar larva. **Fig. 6:** Mature (fourth instar) caterpillar. The larva lacks conspicuous setae. **Fig. 7:** Girdled pupa on hostplant twig.

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of PIERCE (1985). According to her survey, myrmecophilous lycaenids prefer nitrogen-rich hostplants or hostplant tissues, although exceptions from that rule are not uncommon (FIEDLER 1991 a).

Eooxylides tharis is the first member of the subtribe Loxuriti for which larval and pupal vibrations have now been documented. Vibratory signals of the caterpillars do not differ from the pattern widely found in lycaenids (DEVRIES 1991a). We observed larval vibrations also in the related *Yasoda pita, Drupadia ravindra, D. theda* and *Cheritra freja* (FIEDLER & SEUFERT, unpubl.), suggesting that larval vibratory abilities may be ubiquitous in the clade comprising Loxuriti, Cheritriti and Horagiti.

Pupal vibrations were not easy to stimulate in *E. tharis,* and the few stridulatory signals were faint. Instead, the pupae have another defensive behavior: they knock against the substrate when disturbed. I have observed a similar behaviour in pupae of the Miletinae species *Allotinus unicolor* (FIEDLER, unpubl.). Otherwise, this behaviour appears to be unrecorded in lycaenid pupae.

A thorough evolutionary interpretation of the observations presented here must await a phylogenetic analysis of the whole taxonomic group in question. Biological data on genera and species with still unknown life-histories are needed, along with a cladistic analysis of adult, larval and pupal characters. The Loxuriti with their unusual hostplant association and aberrant type of adult feeding pose interesting questions in the framework of a broad comparative approach to lycaenid biology.

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BUCHBESPRECHUNG

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